

THE BEHAVIOR AND MORPHOLOGY OF THE FIG WASPS  
*PEGOSCAPUS ASSUETUS* AND *P. JIMENEZI*<sup>1</sup>:  
DESCRIPTIONS AND SUGGESTED BEHAVIORAL  
CHARACTERS FOR PHYLOGENETIC STUDIES

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Figs (*Ficus* spp., Moraceae) and their pollinator wasps (Agaonidae) are the most intricately coevolved of the plant-insect mutualisms. The necessity of the tiny wasps for good fruit set in cultivated figs [*Ficus carica* (L.)] was recognized over two thousand years ago by Aristotle and his pupil Theophrastus, and the details of pollination in this species were understood by the early part of this century (Condit 1947). It was only fifteen years ago, however, that the tremendous diversity in pollination mechanisms among the approximately 900 species of figs began to be appreciated (Ramirez 1969; Galil and Eisikowitch 1969; Chopra and Kaur 1969). It is generally accepted that each fig species is pollinated by a unique species of fig wasp (Ramirez 1970a; Wiebes 1979). There is much variability in fig inflorescence morphology, which is associated (by host specificity) with variability in fig wasp morphology (Ramirez 1974) and behavior (Galil and Meiri 1981). Although general trends in the mechanism of pollination across subtaxa of *Ficus* and Agaonidae can be inferred from fig inflorescence and fig wasp morphology (Ramirez 1974), the actual details of both pollen collecting and pollination by the wasps have only been studied in a few species. Among the monoecious figs, Galil and Snitzer-Pasternak (1970) studied the pollination of *Ficus religiosa* (L.) by the fig wasp *Blastophaga quadraticeps* (Mayr); Galil and Eisikowitch (1969, 1974) studied *F. sycomorus* (L.) and its pollinator *Ceratosolen arabicus* (Mayr); Joseph and Abdurahiman (1981) described pollination of *F. race-*

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*mosa* (L.) by *C. fusciceps* (Mayr); and Galil et al. (1973) observed the pollination of *F. costaricana* [(Liebman) Miquel] and *F. hemsleyana* (Standley) by *B. estherae* (Grandi) and *B. tonduzi* (Grandi), respectively. Among the dioecious figs, Galil (1973) reported on pollination of *F. fistulosa* (Reinw. ex Bl.) by *C. hewitti* (Waterston); Galil and Neeman (1977) described the details of pollen transfer and pollination in the edible fig *F. carica* (L.) by *B. psenses* (L.); and Okamoto and Tashiro (1981) characterized a remarkable mechanism of pollen transport and pollination in *F. erecta* (Thunberg) by *B. nipponica* (Grandi).

The general features of the pollination cycle of monoecious figs have been described by Galil and co-workers (see above), and reviewed by Janzen (1979) and Wiebes (1979). In this paper I present a detailed description of the pollination cycles of *Ficus aurea* (Nuttall) and *F. citrifolia* (P. Miller), which are pollinated by the fig wasps *Pegoscopus jimenezi* (Grandi) and *P. assuetus* (Grandi), respectively (see Wiebes 1983 for taxonomic discussion of these fig wasp species). The two fig species are closely related members of the monoecious section *Urostigma*. New information presented in this paper includes detailed scanning electron micrographs of the morphology associated with pollination by *Pegoscopus jimenezi*, and detailed descriptions of the behavior during entry into the fig inflorescence, during pollination, and during pollen collecting by *P. jimenezi* and *P. assuetus* in Florida. These behaviors are very similar to those described by Galil et al. (1973) in Costa Rica for the fig wasps *Blastophaga* (= *Pegoscopus*) *estherae* and *B. tonduzi*, which pollinate *Ficus costaricana* and *F. hemsleyana*, respectively. However, clear differences in behavior exist between the fig wasps discussed in this paper and the descriptions of the two Costa Rican species. The usefulness of these behavioral characters for the study of fig wasp phylogeny will be explored in the discussion.

## METHODS

This study was conducted in the Everglades National Park during June 1981. Observations of entry behavior were made in the field with a hand lens. Observations of pollination and pollen-collecting behavior were made by collecting figs at the appropriate stage (see next section), taking the figs into the lab and slicing them open, and observing the wasps with a dissecting microscope. Since no morpho-

logical or behavioral differences relevant to pollination were noticed between the two species studied, the descriptions that follow apply to both fig wasp species.

#### OBSERVATIONS

The details of the flowering and pollination cycle of *Ficus citrifolia* and *F. aurea* will be described in this section. The cycle is presented according to the stages of development of the fig inflorescence (syconium).

##### *Early Development of Syconium and Entry by Pollinator Wasps*

A monoecious syconium is a globular inflorescence containing hundreds of pistillate and fewer staminate florets that line a sealed cavity. The only entrance into this cavity is a series of closely packed, overlapping scales called the 'ostiole.' The young syconia first appear singly, or in pairs, as small protrusions in the leaf axils. Syconia of *F. citrifolia* develop a peduncle 0.5–1.5 mm long, while syconia of *F. aurea* are sessile and subtended by basal bracts. During the early stages of syconium development, the ostiole of *F. aurea* is hidden by two bracts that envelop the entire syconium, while ostiolar scales of *F. citrifolia* are exposed but remain tightly packed, thereby preventing entry by the wasps. As the pistillate florets in the syconia mature, the ostiolar scales of *F. citrifolia* loosen, and the enveloping bracts of *F. aurea* spread to reveal the ostioles. At this stage syconia of *F. citrifolia* are 5–8 mm in diameter, and syconia of *F. aurea* are 4–6 mm in diameter. The syconia are now ready to be entered by the pollinator wasps. Circumstantial evidence suggests that the trees emit a species-specific chemical attractant that indicates receptive syconia (Frank 1983a). Experimental evidence suggests that the pollinator wasps *Pegoscapus assuetus* (reared from *F. citrifolia*) and *P. jimenezi* (reared from *F. aurea*) distinguish between the two fig tree species and, except for rare events, will only enter their own host tree species (Frank 1983a).

The wasps' entry into the syconia is a fixed sequence of behavioral events. A female pollinator wasp (1.2–1.8 mm in length) arrives at and immediately begins antennating a syconium. The wasp assumes a characteristic pose during this "assessment behavior." The legs are extended and the head and sternum are well clear of the syconium surface. The antennae are arched up and the distal portion of the antennae contact the syconium surface perpendicularly, with only

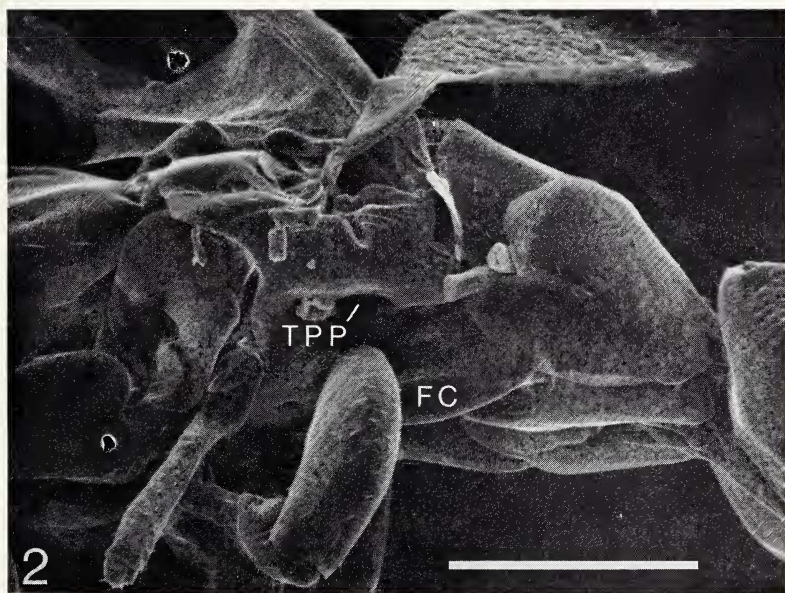
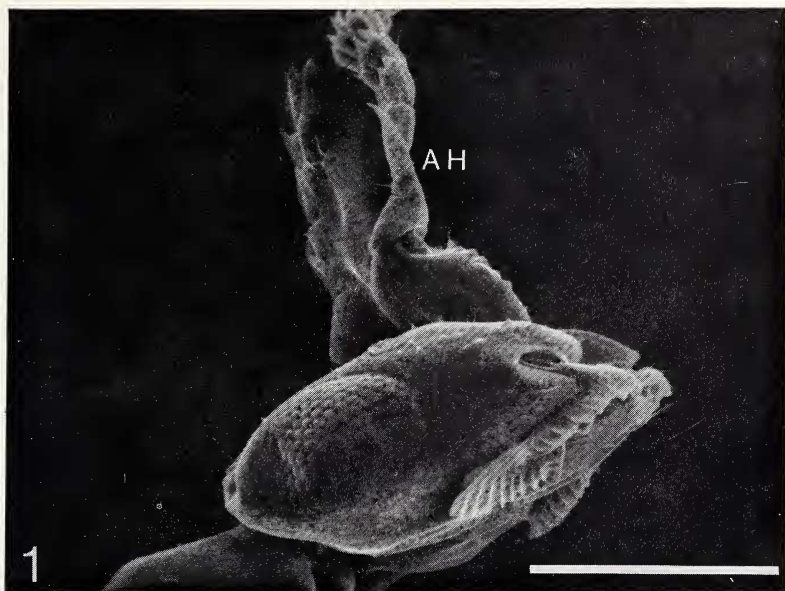
the distal antennal segment actually touching the syconium. The wasp walks over the surface of the syconium in this manner, and does not seem to follow any discernable pattern of movement (such as spending more time near the ostiole). The assessment period lasts from a few seconds to more than five minutes. After assessment the wasp may walk off the syconium and search for other syconia on the same branch, fly away, or begin the next phase of entry.

If the wasp attempts entry, she lowers her antennae, and the distal five or six antennal segments are pressed flat against the syconium surface. The wasp is searching for the ostiole, which she recognizes as a lip on the smooth syconium surface. When she finds the ostiole she loosens the topmost scale with one of the sharp, sclerotized horns on the third antennal segment (Fig. 1). If the upper scale is stuck to the tissue layer below, as is often the case on syconia that have not yet been entered, she approaches at an angle, hooks one horn under the scale, and works the scale free by pushing up with her forelegs and head. When the scale is loosened, she is ready to begin entry. The legs are spread laterally from the body, and the ventral surface of the entire body is flattened against the syconium surface. The antennae are forward and also pressed against the syconium; the wings are raised perpendicularly to the thorax and pressed together; and the abdomen, which has a flexible pleural region and mobile tergites and sternites, is compressed dorso-ventrally. The wasp now pushes her antennae and head under the topmost scale of the ostiole. As the wasp pushes her way forward she arcs her body at approximately a  $120^\circ$  angle. She slowly disappears, and as her thorax passes through the topmost scale her up-raised wings detach. When several wasps enter a single syconium, a tuft of wings can be seen at the entrance to the ostiole. As the female passes under the top scale, she contacts and pushes her head under the lip of the second scale, and continues walking the helical ostiole. The antennae distal to the fourth or fifth segment detach during entry. Also, it has been reported that the unusual mandibles (Fig. 1) are used to aid in entry (Ramirez 1970b). Wasps are not always successful at passing through the ostiole, and are sometimes found dead within the scales of the ostiole, frozen in the remarkably flattened attitude taken during entry.

#### *Female Phase of Syconium; Oviposition and Pollination by Wasps*

After wasps arrive in the central cavity of the syconium they oviposit and pollinate during the day or two before they die. At this





Figures 1 and 2. *Pegoscapus jimenezi*. AH = antennal horn, FC = forecoxa, TPP = thoracic pollen pocket. Bar is 150 $\mu$ m.

stage the pistillate florets are mature and the staminate florets are small and not fully developed ('female-phase' according to Galil and Eisikowitch 1968). The stigmata are intertwined to form a continuous mat (synstigma) that lines the inner surface of the spherical cavity. During entry into the syconium the hypopygium (a movable, sclerotized plate) is flush against the ventral surface of the abdomen, and the abdomen is flattened dorsoventrally. With her rear legs the wasp now kicks the hypopygium down perpendicular to the abdomen (position of hypopygium as in Fig. 16 of Galil and Eisikowitch 1969), and the abdomen becomes slightly compressed laterally. She also uses her rear legs to move the ovipositor shaft from within the ovipositor valves, which protrude distally from the abdomen, to a perpendicular position braced against the triangular hypopygium. The rear legs are also used to groom the ovipositor shaft. When the positioning of the ovipositor is first accomplished the tip of the ovipositor shaft protrudes just beyond the tip of the hypopygium. The female is now prepared to oviposit, and searches by probing the stigmata with the tip of her ovipositor. Eggs are laid by extending the ovipositor down the style and into the ovary of a pistillate floret, where the larva will develop while feeding on the tissues associated with the developing seed or on the seed itself. Within these fig inflorescences there is polymorphism in style length among the pistillate florets. The fig wasp's ovipositor is long enough to reach down shorter-styled florets and into the ovary, but is usually not long enough to reach down longer styles and into the ovary. Thus the short-styled florets usually produce wasps, while the long-styled florets usually produce seeds. While ovipositing the wasp stands on all six legs, with the body and head well clear of the stigmata, and the tip of the hypopygium just touching the top of the stigma being oviposited in. Oviposition lasts 105–300 seconds ( $n=9$ ).

The wasps usually spread pollen nearby after each oviposition. Pollination consists of four behaviors: (i) loosening a few pollen grains from the caches kept in special sternal mesothoracic pockets, (ii) collecting these loose pollen grains in scoopers (arolia) on the foretarsi, (iii) transferring the pollen from the arolia to the surface of the hypopygium, and (iv) dragging the pollen-dusted hypopygium over the stigmata.

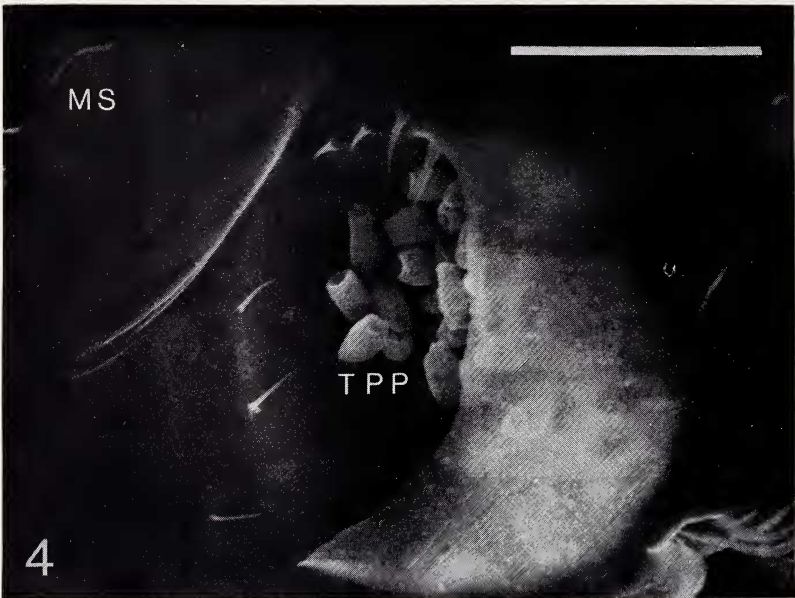
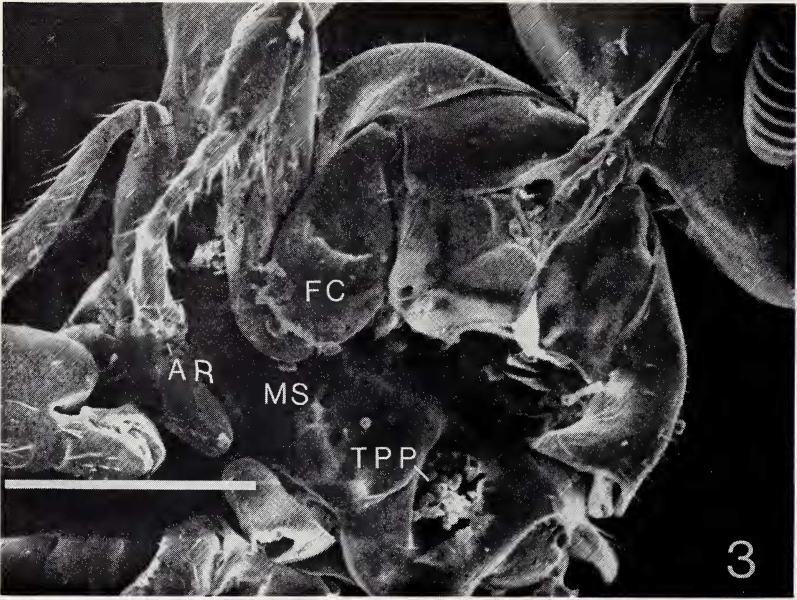
(i) Loosening pollen from the thoracic pockets. Towards the end of an oviposition act the wasp lifts her forelegs and begins a rhythmic motion with the front part of her body. The pronotum and head

slide forward and down—the pronotum dropping about  $70^\circ$  from horizontal while sliding over the mesonotum as an airplane-wing flap. The forecoxae move up flush against the mesosternum (Figs. 2,3); simultaneous with the pronotum and head moving forward and down, the forecoxae slide posteriorly then laterally over the mesosternum. First the forecoxae are moved back so that they are medial to the pollen pockets, which are located laterally on the mesosternum (Figs. 3,4). (These pockets are loaded with pollen; the manner in which the wasp obtains this pollen is described in the next section.) The forecoxae are then moved laterally until they are over the pollen pockets, and a stiff row of bristles on the coxal-femoral joints is at the posterior ends of the pockets (Figs. 5,6). The wasp then moves her pronotum and head up and simultaneously slides the coxae forward through the pockets. This causes the coxal-femoral bristles moving through the pockets to act as rakes, which loosen a few pollen grains and move them to the forward edge of the pockets. An alternative interpretation of the action of the coxal rake is that it scoops pollen out of the mesothoracic pockets and into the coxal pockets (corbiculae, Fig. 7). The two interpretations are discussed below in (ii).

(ii) Collecting pollen grains in arolia. After pollen is loosened from the mesothoracic pockets, the tibiae are quickly moved upwards until they are flattened against the femorae, such that both the tibiae and femorae are parallel to the stigmal surface and pulled in close to the body. The arolia at the tips of the foretarsi open into membranous scoops, and are very quickly brushed back and forth 3–5 times ( $n=6$ ) in order to collect pollen. It is difficult to observe exactly where the pollen is collected. On three occasions I saw an arolium scoop pollen from the front edge of a thoracic pocket. In the remainder of my observations (approximately 50 occasions) I was unable to determine whether the arolium obtained pollen from within or near the thoracic pocket, or from the coxal pollen pockets, as reported for *Blastophaga estherae* and *B. tonduzi* by Galil et al. (1973). Based on the structure of the coxal rake (Figs. 5,6) and pattern of movements in (i), and my observations, I favor the interpretation that the pollen is usually collected by the arolia in or near the mesothoracic pockets.

(iii) Transferring pollen from arolia to hypopygium. After pollen is collected in the arolia, the wasp reaches down with her forelegs and wipes the arolia upwards along the anterior edge of the hypopy-





Figures 3 and 4. *P. jimenezi*. FC = forecoxa, TPP = thoracic pollen pockets, MS = mesosternum, AR = arolium; note lateral pocket membrane in Fig. 4. Bar is 150 $\mu$ m in Fig. 3, 40  $\mu$ m in Fig. 4.

gium, this plate being in the down position, perpendicular to the abdomen.

(iv) Dragging the pollen-dusted hypopygium over the stigmata. The tip of the hypopygium is kept just above the stigmatal surface during oviposition, and during steps (i)–(iii) described above. After being dusted with pollen from the arolia, the tip of the hypopygium is pushed down into the stigmata as the wasp begins to walk and search for a new floret in which to oviposit. Time spent searching between pollination and the beginning of the next oviposition ranged from 15 seconds to 150 seconds ( $n=5$ ).

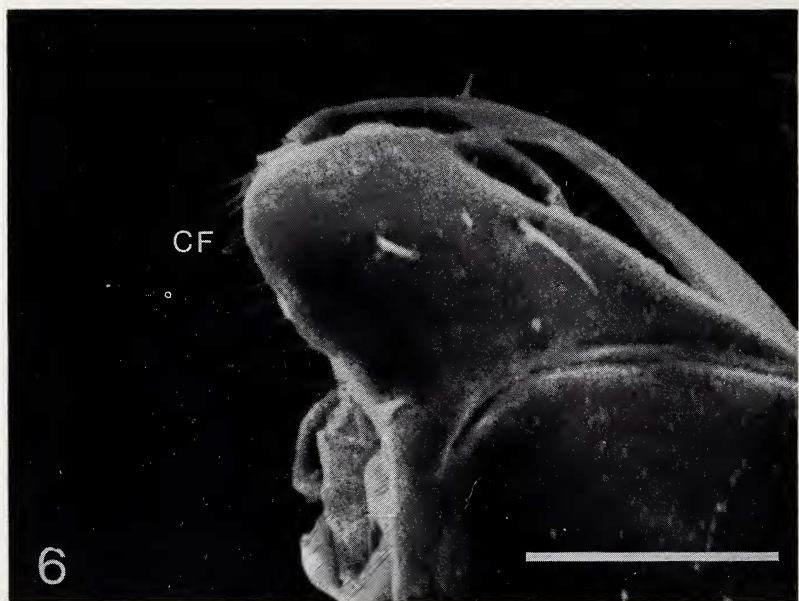
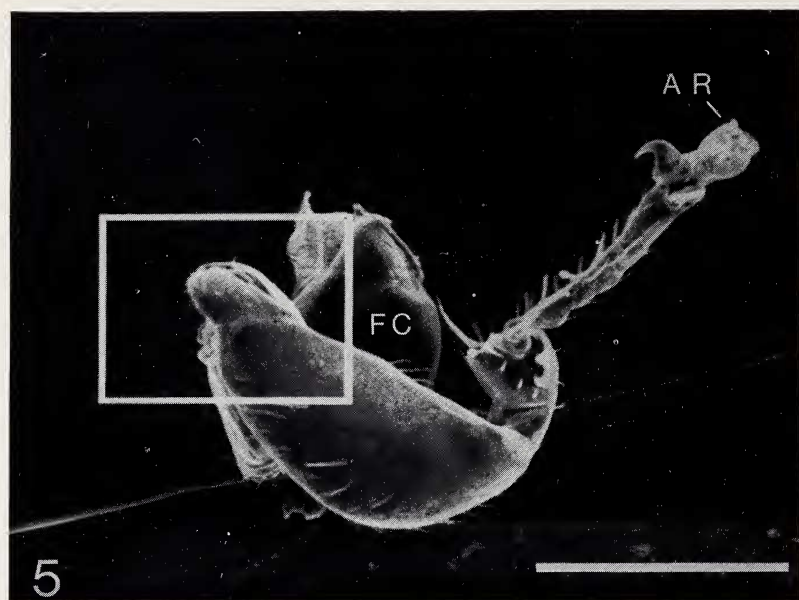
Two or more wasps often oviposit and pollinate simultaneously within a syconium (Frank 1983a). Among the approximately one hundred syconia I opened with two or more wasps ovipositing simultaneously, I never observed any sort of behavior that might be called 'aggressive.' Ramirez (1970b) has reported that New World fig wasps are aggressive towards each other during oviposition and pollination, but he did not specify in which species he actually observed aggressive behavior.

After females of *P. jimenezi* lay 23–130 eggs each ( $n=9$ ), or females of *P. assuetus* lay 9–110 eggs each ( $n=18$ ) (Frank 1983a), the wasps die in the central cavity of the syconium. The larvae and seeds develop—this period is referred to as the 'interfloral phase' of syconium development (Galil and Eisikowitch 1968).

#### *Male Phase of Syconium; Mating and Pollen Collecting by Wasps*

After 27–32 days the central cavity swells. The staminate florets are now mature (hence 'male phase' according to Galil and Eisikowitch 1968), and the randomly located anthers are clearly visible within the cavity. The male progeny emerge from the ovaries of the pistillate florets in which they developed. The percentage of males among the progeny generation is much less than the percentage of females (typically 5–20% males). Further, there is a strong positive correlation in *P. assuetus* between the number of females ovipositing in a syconium and the percentage of males in the progeny generation (Frank 1983a,b). The wingless males have reduced eyes and little pigmentation. Their legs are short and thick, and their abdomens curl under the ventral surface of the thorax and head (Fig. 8). The males wander through the labyrinth-garden of swollen pistillate and now mature staminate florets, searching for females. These females are mature, but remain quiescent in the floral ovaries in





Figures 5 and 6. Right foreleg of *P. jimenezi*. AR = arolium, FC = forecoxa, CF = coxal-femoral rake. Fig. 6 is an enlargement of the box in Fig. 5. The bar is 150 $\mu$ m in Fig. 5, 30 $\mu$ m in Fig. 6.

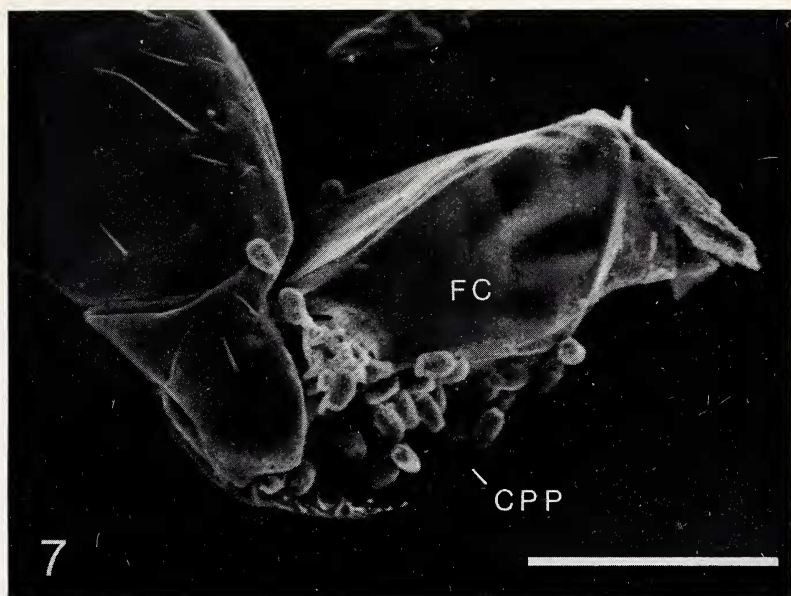


Figure 7. Left foreleg of *P. jimenezi*. FC = forecoxa, CPP = coxal pollen pocket. The bar is 60 $\mu$ m.

Figure 8. Male of *P. jimenezi*. Bar is 400 $\mu$ m.

which they developed. When a male finds an ovary containing a female, he chews a hole, inserts his telescoping abdomen, and mates with the female. The many males within the confined cavity walk into, over, and on top of each other, but I know of no report of aggressive interactions among male fig wasps. Nonrandom patterns of male movement within the syconium during mating have been discussed by Frank (1983a, 1985).

After a one to two day mating period, one or more males chew(s) an exit tunnel through the wall of the syconium. Following completion of the exit tunnel, the females widen the hole in the floret ovary created by the male during mating, and then struggle free into the central cavity of the syconium. Their wings are stuck to the abdomen and the pupal skin still covers their heads. They quickly groom their wings free by passing their rear legs between the wings and upper abdomen while simultaneously removing their pupal skin from their head with their forelegs.

After grooming, the females immediately begin to search for an anther that still contains pollen. When an anther is found the dehiscence slit is opened by passing one of the sclerotized horns on the third antennal segment (Fig. 1) through the length of the slit. Then the anterior portion of the head is placed within the anther, with the mandibles loosening the pollen grains, and the pronotum is slid forward and down. Next a foreleg (e.g., right foreleg) is stretched forward and placed in the anther, and the arolium scoops up a load of pollen. This load of pollen is moved upwards to the left forecoxa, and the left foreleg is simultaneously extended towards the anther. As the left foreleg is extended the left coxa is moved slightly away from the underside of the body exposing the pocket on the coxa (Fig. 7). The load of pollen from the right arolium is placed in the pocket of the left coxa. Next the right foreleg is extended again to pick up another load of pollen, and the pollen load of the left foreleg is placed on the right coxal pocket. After 16–32 loads ( $n=7$ ) have been collected, the coxal pockets are bulging with pollen. Pollen is also in the intersegmental region between the pro- and meso-sterna.

The pollen is now moved from the coxal pockets and sternal region to the mesothoracic pockets. The sequence of movements is quite similar to those described above for pollen raking during pollination. The wasp lifts her head from the anther. The coxae are pressed against the prosternum, forming about a  $45^\circ$  angle with the medial line of the sternum. The coxae are then brushed posteriorly

across the intersegmentus, while maintaining their angle relative to the median sternal line. This movement of the coxae is accomplished by sliding the pronotum forward and down, which causes the prosternum to form about an  $80^\circ$  angle with the mesosternum. The coxae are now against the flattened medial region of the mesosternum (Fig. 3). Next the coxae are brushed laterally over the mesothoracic pockets (Figs. 9,10). The lateral membranous flap of the pockets (Fig. 4) may aid in scooping the pollen from the coxal pockets. The coxae are brought forward again when the pronotum is raised; thus the coxae are moved in a circular motion. The sequence is usually repeated 3–8 times, although the observed range was 2–34 ( $n=15$ ). Sometimes two or three females will collect pollen from the same anther. If only a small amount of pollen is collected, the wasp will find another anther and repeat the pollen collecting sequence.

After collecting pollen the wasps leave the syconium through the exit tunnel and quickly take to the air, perhaps because predaceous ants of the genus *Pseudomyrmex* are often waiting for escaping wasps. Those wasps that successfully find receptive syconia begin the cycle again.

#### DISCUSSION

The use of behavioral characters in systematics has been reviewed and discussed several times (e.g., Lorenz 1950; Evans 1952; Mayr 1958; Alexander 1962; Blair 1962; Atz 1970; Hinde 1970). Three examples are Lorenz's (1941) phylogeny of ducks and geese (Anatidae) based solely on behavioral characters, leading to Delacour and Mayr's (1945) revision based on both morphology and behavior, Evans' (1952) work on the comparative behavior and systematics of spider wasps (Pompilidae), and van den Assem et al.'s (1982) subdivision of *Melittobia* (Eulophidae) based on mating behavior. Also, several workers have noted a reasonable congruence between inferred phylogenies based on behavior and those based on morphology (e.g., Speith 1952 for *Drosophila*; Crane 1952 for mantids; and Michener et al. 1978 for Apidae).

The phylogeny of the Agaonidae is controversial (Wiebes 1982), and much work remains. Behavioral characters have not been used in fig wasp systematics, simply because there is not enough comparative information available. Fig wasps seem ideal for comparative studies of behavior, since so much of their behavior is extremely



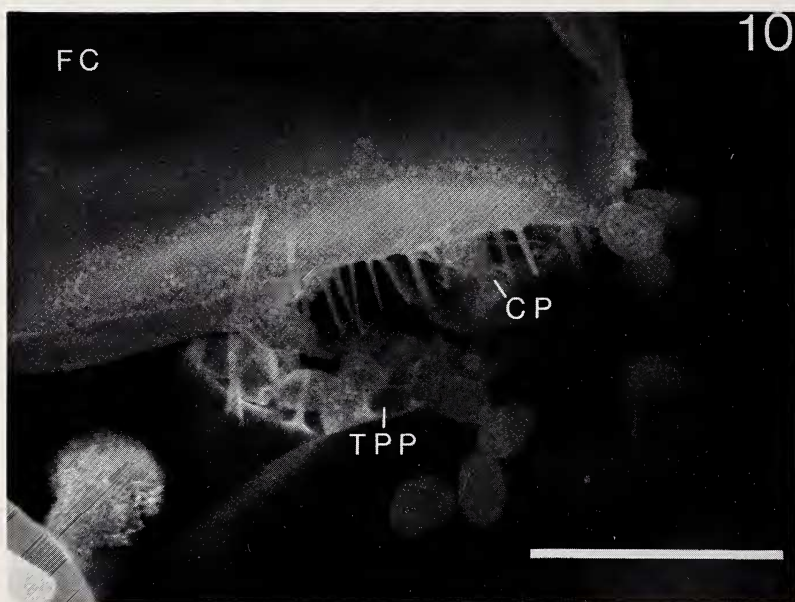


Figure 9 and 10. Pro- and meso-sterna of *P. jimenezi*. TPP = thoracic pollen pocket, FC = forecoxa, CP = coxal pollen brush. Fig. 10 is an enlargement of the box in Fig. 9. The bar in Fig. 9 is 100 $\mu$ m, 30 $\mu$ m in Fig. 10.



stereotyped and easily observed, and since the wasps' morphological structures make sense only in light of their associated motor patterns. Based on the few species reviewed below, it seems that behavioral information will be of some value in sorting out the systematics of this difficult group.

The sequence of behaviors during pollen collecting and during oviposition and pollination are compared in Table 1 between the Florida wasps *Pegoscapus assuetus* and *P. jimenezi* and the Costa Rican wasps *P. tonduzi* and *P. estherae*. There are three reasons for presenting this comparison. First, it highlights the extreme similarity in behavior among these four species. Second, it points out that clear differences in behavior do exist, and that these differences may be good characters for phylogenetic inference, or at least that a congruence between established phylogenies and behavioral differences may be observed (see also Table 2). Finally, these comparisons show the sort of detailed description that will be necessary if behavioral characters are to prove valuable, and will hopefully stimulate fig-watchers to begin assembling the necessary comparative information so that this story of morphological and behavioral coevolution can be written.

#### ACKNOWLEDGMENTS

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Table 1. Comparison of oviposition and pollination, and of pollen collecting between *Pegoscapus assuetus* and *P. jimenezi* (described in this paper) and *P. tonduzi* and *P. estherae* (Galil et al. 1973). All these wasps pollinate figs of the monoecious section *Urostigma*. These descriptions are schematic and are only meant to highlight obvious similarities and differences. See original descriptions for more details.

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*Pegoscapus assuetus* and *P. jimenezi*

OVIPOSITION AND POLLINATION: Probe synstigma with ovipositor → insert ovipositor down style → oviposit → loosen pollen grains in mesothoracic pockets with coxal-femoral rake → collect pollen in arolia from thoracic or coxal pollen pockets<sup>1</sup> → wipe pollen from arolia onto hypopygium<sup>2</sup> → drag hypopygium over synstigma.

POLLEN COLLECTING: slit anther with antennal horn → place anterior portion of head in anther → [right arolium scoops pollen from anther<sup>3</sup> → right arolium pulled towards ventral surface of body, left arolium simultaneously extended → left arolium scoops pollen from anther, right arolium simultaneously places pollen load on exposed left coxal pocket → right arolium extended to scoop pollen load from anther, left arolium simultaneously places pollen load on exposed right coxal pocket] → repeat brackets 16–32 (n=7) times → forecoxae rubbed posteriorly over mesosternum, then laterally over mesothoracic pollen pockets, transferring most of pollen to these pockets.

*Pegoscapus tonduzi* and *P. estherae*

OVIPOSITION AND POLLINATION: Probe → insert → oviposit → loosen pollen → collect pollen into arolia<sup>1</sup> → release pollen by rubbing arolia together above (not touching) synstigma<sup>2</sup>.

POLLEN COLLECTING: slit anther → head in anther → arolia alternately lift pollen (up to 40 times) towards ventral surface of thorax → some pollen pressed into intersegmental chamber by forecoxae → coxae rubbed over mesosternum and pollen pockets, filling mesothoracic pockets, repeated several times.

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<sup>1</sup>It is not known whether the arolia usually collect pollen from the thoracic pockets, or from the coxal pockets. My interpretation of *P. assuetus* and *P. jimenezi* is that pollen is taken directly from the thoracic pockets; Galil et al. (1973) suggest that the arolia collect pollen from the coxal pockets in *P. tonduzi* and *P. estherae*.

<sup>2</sup>This is the clearest difference between the two pairs of species.

<sup>3</sup>Choice of the right foreleg instead of the left is arbitrary, and only for purposes of illustration.

Table 2. Comparison of oviposition and pollination, and of pollen collecting, between *Ceratosolen arabicus* (Galil and Eisikowitch 1969, 1974), *C. hewitti* (Galil 1973), and *C. fusciceps* (Joseph and Abdurahiman 1981), and *Blastophaga quadraticeps* (Galil and Snitzer-Pasternak 1970). These descriptions are schematic and are only meant to highlight obvious similarities and differences. See original papers for more details.

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*Ceratosolen arabicus*, *C. hewitti*<sup>1</sup>, and *C. fusciceps*

**OVIPOSITION AND POLLINATION:** Probe synstigma with ovipositor → insert ovipositor down style → oviposit and simultaneously tremble and lower head to vigorously bite the stigmata within reach → forelegs lifted, forecoxae pressed to thorax → [femur and tarsi become parallel, and are moved together downward and posteriorly → when femur-tarsi are at right angles to coxae, arolia are moved into open pocket and collect pollen] → repeat brackets several times → tarsi are unfolded downward and touch stigmata → retract ovipositor → repeat entire cycle.

**POLLEN COLLECTING:** Pollen pockets have membranous covers, as opposed to open pockets of *Pegoscapus* spp. (see Fig. 4). Male wasps detach anthers → females emerge from flowers in which they developed → grasp anther → search for dehiscence slit → widen slit with mandibles and antennae → pollen lifted from anther to underside of thorax with arolia (32–98 alternate lifting,  $n=3$ ) → thorax curved so that covering membranes of thoracic pockets stand out → pollen pushed into thoracic pockets with combs on forecoxae → males chew exit tunnel → females leave fig.

*Blastophaga quadraticeps*

**OVIPOSITION AND POLLINATION:** As in *C. arabicus*, except body is almost static during oviposition, head is motionless and no biting of synstigma occurs.

**POLLEN COLLECTING:** Pockets have membranous covers. Male wasps chew exit tunnel → females emerge from flowers in which they developed → approach anther → crumble pollen with base of antennae and mandibles → forelegs touch anthers, then move up and back along inner margin of thoracic pocket, repeated several times, motion identical to reverse of pocket unloading in *C. arabicus* → leave fig through exit tunnel with thoracic pockets full of pollen.

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<sup>1</sup>*C. hewitti* pollinates a dioecious fig, while the other three wasps described here pollinate monoecious figs.

## LITERATURE CITED

ALEXANDER, R. D.

1962. The role of behavioral study in cricket classification. *Syst. Zool.* **11**: 53-72.

ASSEM, J. VAN DEN, H. A. J. IN DEN BOSCH, AND E. PROOY.

1982. *Melittobia* courtship behaviour: a comparative study of the evolution of a display. *Neth. J. Zool.* **32**: 427-471.

ATZ, J. W.

1970. The application of the idea of homology to behavior. In S. Coopersmith (ed.) *Development and the evolution of behavior*. Freeman, San Francisco. pp. 53-74.

BLAIR, F. W.

1962. Non-morphological data in Anuran classification. *Syst. Zool.* **11**: 72-84.

CHOPRA, R. N., AND H. KAUR.

1969. Pollination and fertilization in some *Ficus* species. *Beitr. Biol. Pflanzen* **45**: 441-446.

CONDIT, I. J.

1947. The fig. *Chronica Botanica Co.*, Waltham, Massachusetts.

CRANE, J.

1952. A comparative study of innate defensive behavior in Trinidad mantids (Orthoptera, Mantoidea). *Zoologica* **37**: 259-294.

DELAOUR, J. AND E. MAYR.

1945. The family Anatidae. *Wilson Bull.* **57**: 1-55.

EVANS, H. E.

1952. Comparative ethology and the systematics of spider wasps. *Syst. Zool.* **2**: 155-172.

FRANK, S. A.

- 1983a. Theoretical and empirical studies of sex ratios, mainly in fig wasps. M.S. thesis, University of Florida.

- 1983b. A hierarchical view of sex-ratio patterns. *Fla. Ent.* **66**: 42-75.

1985. Are mating and mate competition by the fig wasp *Pegoscapus assuetus* (Agaonidae) random within a fig? *Biotropica* **17**(1): in press.

GALIL, J.

1973. Pollination in dioecious figs. Pollination in *Ficus fistulosa* by *Ceratosolen hewitti*. *Gdns' Bull. Singapore* **26**: 303-311.

GALIL, J., AND D. EISIKOWITCH.

1968. On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* **49**: 259-269.

1969. Further studies on the pollination ecology in *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae). *Tijdschr. Ent.* **112**: 1-13.

1974. Further studies on pollination ecology in *Ficus sycomorus*. II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. *New Phytol.* **73**: 515-528.

GALIL, J., AND L. MEIRI.

1981. Number and structure of anthers in fig syconia in relation to behaviour of the pollen vectors. *New Phytol.* **88**: 83-87.

GALIL, J., AND G. NEEMAN.

1977. Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.* **79**: 163–171.

GALIL, J., W. RAMIREZ B., AND D. EISIKOWITCH.

1973. Pollination of *Ficus costaricana* and *F. hemisleyana* by *Blastophaga estherae* and *B. tonduzi* (Agaonidae) in Costa Rica. *Tijdschr. Ent.* **116**: 175–183.

GALIL, J., AND Y. SNITZER-PASTERNAK.

1970. Pollination in *Ficus religiosa* L. as connected with the structure and mode of action of the pollen pockets of *Blastophaga quadraticeps* Mayr. *New Phytol.* **69**: 775–784.

HINDE, R. A.

1970. Animal behaviour: a synthesis of ethology and comparative psychology. McGraw-Hill, New York.

JANZEN, D. H.

1979. How to be a fig. *Annu. Rev. Ecol. Syst.* **10**: 13–51.

JOSEPH, M., AND V. C. ABDURAHIMAN.

1981. Oviposition behavior of *Ceratosolen fusciceps* Mayr (Agaonidae: Hymenoptera) and the mechanism of pollination of *Ficus racemosa* L. *J. Bombay Nat. Hist. Soc.* **78**: 287–291.

LORENZ, K.

1941. Vergleichende Bewegungsstudien an Anatiden. *J. f. Ornithol. Suppl.* **89**: 194–293.

1950. The comparative method in studying innate behaviour patterns. *Sym. Soc. exp. Biol.* **4**: 221–268.

MAYR, E.

1958. Behavior and systematics. In A. Roe and G. G. Simpson (eds.) *Behavior and Evolution*. Yale Univ. Press. pp. 341–362.

MICHIENER, C. D., M. L. WINSTON, AND R. JANDER.

1978. Pollen manipulation and related activities and structures in bees of the family Apidae. *Univ. Kansas Sci. Bull.* **51**: 575–601.

OKAMOTO, M., AND M. TASHIRO.

1981. Mechanism of pollen transfer and pollination in *Ficus erecta* by *Blastophaga nipponica*. *Bull. Osaka Mus. Nat. Hist.* **34**: 7–16.

RAMIREZ, B. W.

1969. Fig wasps: mechanisms of pollen transport. *Science* **163**: 580–581.

- 1970a. Host specificity of fig wasps (Agaonidae). *Evolution* **24**: 680–691.

- 1970b. Taxonomic and biological studies of neotropical fig wasps (Hymenoptera: Agaonidae). *Univ. of Kansas Sci. Bull.* **39**: 1–44.

1974. Coevolution of *Ficus* and Agaonidae. *Ann. Missouri Bot. Gard.* **61**: 770–780.

SPEITH, H. T.

1952. Mating behavior within the genus *Drosophila* (Diptera). *Bull. Am. Mus. Nat. Hist.* **99**: 399–474.



WIEBES, J. T.

- 1979. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.* **10**: 1-12.
- 1982. The phylogeny of the Agaonidae (Hymenoptera, Chalcidoidea). *Nether. J. Zool.* **32**: 395-411.
- 1983. Records and descriptions of *Pegoscapus* Cameron (Hymenoptera Chalcidoidea, Agaonidae). *Proc. Kon. Ned. Akad. Wetensch. (C)* **86**: 243-253.